

Life history consequences of social complexity: a comparative study of ground-dwelling sciurids

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We examined life-history consequences of increased social complexity in ground-dwelling sciurid rodents. We derived a continuous metric of social complexity from demographic data. Social complexity increased with the number of age-sex "roles" that interacted in a social group. Data were analyzed by computing phylogenetically independent contrasts and by using phylogenetic autocorrelation to estimate and then remove the maximum amount of variation in life-history variables that could be attributed to phylogenetic similarity. Analyses that incorporated estimates of phylogeny generated consistent results. As social complexity increased, a smaller proportion of adult females bred, there was a greater time to first reproduction, litter size decreased, and there was greater first-year offspring survival. Social complexity influenced neither gestation nor lactation time. Thus, social complexity has costs in terms of a reduction in the annual per-capita number of offspring produced but benefits in terms of enhanced offspring survival. **Key words:** *Cynomys*, costs and benefits of sociality, life history, *Marmota*, social complexity, *Spermophilus*. [*Behav Ecol* 9:8–19 (1998)]

Sociality involves benefits and costs of forming aggregations and of behaviors in the aggregations. Generally, animals are hypothesized to aggregate to reduce predation risk and/or because of the distribution of critical resources (Alexander, 1974). Social structure and social behaviors may further increase the benefits of aggregation (Alexander, 1974). Thus, behaviors such as alarm calling (Sherman, 1977), allogrooming (Hart and Hart, 1992), dominance relationships (Bernstein, 1981), food calling and sharing (e.g., Benz, 1993; Goodall, 1986; Hauser 1996), helping (e.g., Brown, 1987), individual recognition (Wrangham, 1983), mating systems (Emlen and Oring, 1977), and a variety of other social behaviors can evolve and be elaborated once social groups have formed. Aggregation has its costs: more competition for scarce resources (Wrangham et al., 1993); monopolization of resources by dominant animals (Wrangham, 1981); increased aggression (Walters and Seyfarth, 1986); increased risk of parasite and disease transmission (Brown and Brown, 1986; Mooring and Hart, 1992); attraction of more predators (Kruuk, 1964; Pienkowski and Evans, 1982); increased reproductive competition, which may lead to infanticide (Hoogland, 1995); and prevention, delay, or an influence on reproduction in certain animals (e.g., Abbott, 1987; Packer et al., 1995; Wasser and Barash, 1983). These and other factors may lead to variation in reproductive success among group-living animals.

Each of these specific benefits and costs emerges from sociality. While not specifically stated and defined, more of these costs and benefits are assumed to emerge as social complexity increases. In this paper we explicitly address the question of costs and benefits of increased social complexity. We focus on ground-dwelling sciurid rodents (marmots, *Marmota* spp.; prairie dogs, *Cynomys* spp.; and ground squirrels, *Spermophilus* spp.) and review the literature to summarize a series of life-history variables. Ground-dwelling sciurids are an ideal taxon about which to ask questions regarding the evolutionary impacts of social variation. A large body of literature exists on

social variety in marmots, prairie dogs, and ground squirrels (e.g., Barash, 1989; Bibikow, 1996; Hoogland, 1995; Murie and Michener, 1984). Social organizations range from species in which individuals disperse immediately after weaning and live more or less solitary lives, to species in which individuals exhibit delayed dispersal and in which overlapping generations of individuals share a home range and interact amicably. Moreover, species can be placed objectively along a continuum of social complexity (see below and Blumstein and Armitage, 1997). We ask the following six life-history questions: Does social complexity influence (1) the percentage of adult females who breed, (2) the time to first reproduction, (3) gestation time, (4) average litter size, (5) lactation time, and (6) percent juvenile survival to age 1?

Defining complexity

The term "complexity" is often used but rarely defined explicitly (McShea, 1991, 1996). Complexity can be explicitly defined using information theory (Shannon and Weaver, 1949). A more complex system requires more information (specifically "binary units") to be fully described than does a less complex system. With respect to sociality, a species with 10 different social behaviors is more complex than one with a single social behavior because more discrete behaviors can be used in more ways (Bonner, 1988). As the number of interacting individuals increases, there is an opportunity for more social interactions and for more social behaviors (e.g., solitary animals do not need a repertoire of sophisticated dominance behaviors). We might assume that a species typically living in large social groups is more complex than a species typically living in smaller social groups. Group size has been used as a measure of sociality (e.g., Eisenberg, 1981; Janson and Goldsmith, 1995), yet social group size alone is an inadequate metric of social complexity because social behavior involves relationships between individuals, and the diversity of these relationships is not described by simply using group size. Because social systems are typically defined categorically (e.g., "monogamous" versus "polyandrous" versus "polygynous"), it is not immediately obvious how to objectively compare different social systems with respect to varia-

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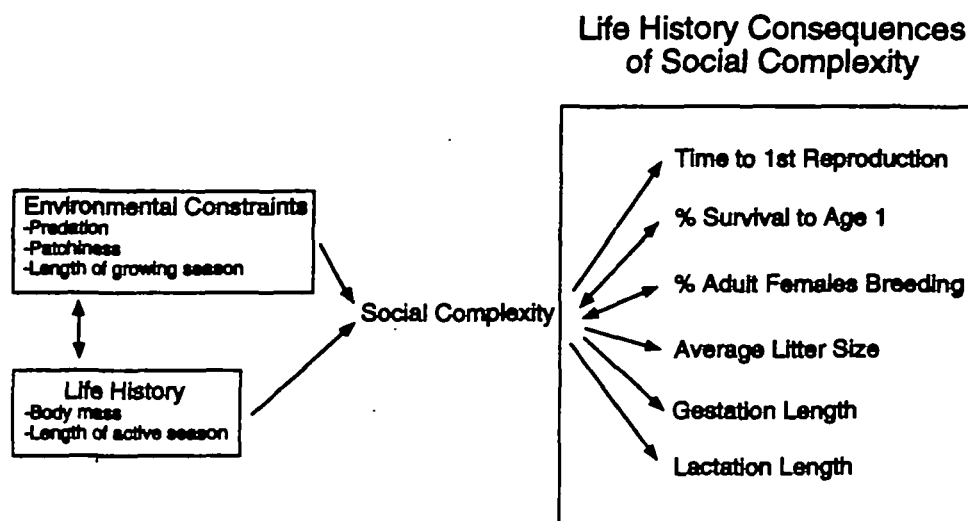


Figure 1
Some causes and consequences of social complexity. Causality is justified in text.

tion in complexity. A new metric of social variation is required to specifically quantify complexity.

Social complexity emerges from groups of individuals that interact over some time. Within a group, animals may be described as having certain "roles"—socially expected behavior patterns (Blumstein and Armitage, 1997). For instance, there may be a dominant and a subordinate role. Or, there may be a breeder and a nonbreeder role. An individual's role may change over time. To quantify social complexity, it is crucial to identify roles. Practically, this is quite difficult to do in a comparative study because different studies emphasize different aspects of sociality. However, it is possible to define "demographic roles" (e.g., adult female/adult male, subadult female/male, etc.), and these demographic roles should describe the potential for more complex social behavior.

Social complexity also implies social flexibility, and intra-specific social variation is often adaptive (Lott, 1991). Consider two species with two demographic roles. Each of these roles has the same mean size (e.g., six adult males and six adult females), but the species differ in the variance around these means. Because it requires more information to describe a more variable system than a less variable system, the more variable system is more complex. For instance, if males always aggregate in groups of six (i.e., no variation), then it requires little information to describe male social structure—males aggregate in groups of six. Additional variation requires more information to describe a demographic role. Socially, a species that must be able to adapt to different types and numbers of potential social partners is more complex than one with a fixed number of social partners. Thus, social complexity increases with more demographic roles and when the number of individuals in a given role varies. It is also likely that more precisely defined roles will reveal more variation in social complexity. For instance, the six males may or may not have dominance relationships.

We previously defined social complexity using information theory (Blumstein and Armitage, 1997). We focused on social group structure, where we defined a social group as a group of individuals that remain together and interact more with each other than with other conspecifics (Slobodchikoff and Shields, 1988; Wilson, 1975). For ground-dwelling sciurids, animals in the same social group have extensively overlapping home ranges, and animals may share sleeping burrows during much of the year. In suitable habitat, there may be many contiguous social groups (e.g., a prairie dog "town," or a ground squirrel "colony"). We focus on the individual social units within this higher level aggregation because the number of

contiguous social groups will be influenced strongly by the amount of suitable habitat and by a species' total energetic requirements.

Sciurid demographic roles include adult females/males, 2 year olds, yearlings, and juveniles. Not all species have all five roles. For each role a species had, we summarized the frequency distribution of the numbers of animals (i.e., 0 males in 1 group, 1 male in 20 groups, 2 males in 36 groups, 3 males in 0 groups, etc.). From frequency distributions like these, we quantified the amount of information required to describe each demographic role.

$$H(X)_i = -\sum p(i) \log_2 p(i) \quad (1)$$

defines the number of bits of information required to describe a role, $H(X)_i$, given the relative frequency, $p(i)$, of each of the discrete counts (i.e., 0, 1, 2, 3, ...) of animals in that role. We summed the $H(X)_i$ for each role to get an $H(X)_t$, the total number of bits required to describe a species given the number of demographic roles. Because timing of natal dispersal from sciurid social groups varies, we multiplied $H(X)_t$ by a number reflecting the time to natal dispersal (1 = dispersed as juveniles, 2 = dispersed as yearlings, 3 = dispersed at age two or older), and log transformed the product to generate a number, SC_d , a value reflecting social complexity. In doing so we are aware that sciurids with more demographic roles also have delayed dispersal. In fact, this multiplication has limited effects on our data set. The multiplication emphasizes the potential importance of kin structure, a key characteristic of sociality and social complexity.

At first glance, our use of social complexity to study life history consequences may appear circular. Our metric of social complexity, SC_d , is largely determined by a species' demographic structure and thus is influenced by variables such as the time to natal dispersal. However, there is no a priori reason that more socially complex species should delay dispersal. The ground-dwelling sciurids we studied increased complexity largely by delaying dispersal, but social complexity could also increase via immigration and not delayed dispersal (e.g., imagine a college dormitory, a very complex "social group," formed exclusively by immigration).

Given our metric of social complexity, we focused on life-history consequences of social complexity and thereby imply causal relationships between social complexity and each of our life-history variables. Studying causal processes is difficult with some comparative analyses of continuous data because the sequence of change is not specified (e.g., Promislow, 1996; Ridley and Grafen, 1996). Figure 1 specifies several potential

causes and consequences of social complexity. Complex social behavior is traditionally expected when there are environmental constraints (e.g., Emlen, 1991; Emlen and Vehrenkamp, 1983) that may directly, or indirectly (acting through life history variables) influence social complexity. Direct factors such as predation (Alexander, 1974; Hoogland, 1995), habitat patchiness (e.g., Michener, 1984), and growing season length (e.g., Armitage, 1981) may select for aggregation, leading to an increase in social complexity. Life-history variables such as body mass (Armitage, 1981; Barash, 1989; Bekoff et al., 1981) or the length of the active season for hibernating mammals (Armitage, 1981; Barash 1989) may also influence social complexity. Interestingly, although not the topic of this paper, we found no relationship between active season length (number of months active above ground and not hibernating) or body mass (minimum adult female body mass) on social complexity in phylogenetic analyses.

In this paper we focus on six life history consequences of social complexity. We had a priori expectations that social complexity could influence them all (Armitage, 1981, 1996). However, causality might be symmetric for at least two of these variables: percent survival to age 1 (after controlling for body mass) and the percentage of adult females who breed (after controlling for body mass). If more individuals survive to age 1, and if dispersal is delayed, then social complexity will increase because the number of age/sex classes increases. If more adult females breed, and if these breeding females are in the same social group, then social complexity may increase. Alternatively, if only older adult females breed while younger females remain in the social group, social complexity may increase. For these two variables, a potential unimplemented solution would be to hypothesize specific causal models (e.g., Asher, 1983) and study the independent paths to and from these two variables via social complexity. Currently, skeptics may interpret the results as demonstrating a strong, noncausal relationship between social complexity and these two life-history variables.

METHODS

Comparative data set

To calculate social complexity, we reviewed the literature for studies that reported demographic information. A number of studies did not report litter size distribution. If a mean and standard deviation were reported, we assumed litter size was normally distributed to estimate litter size distribution. We obtained sufficient data to calculate social complexity for 25 species: 7/14 marmots, 5/5 prairie dogs, and 13/38 *Spermophilus* ground squirrels. For these 25 species, we summarized information on the following seven life-history variables, selected both because they are generally available and because they have been used in previous comparative studies (see Appendix for comparative data and associated references):

1. Percent adult females who breed. This was generally calculated as a simple average. It was calculated as a weighted average in a few cases where there was age-specific variation and large sample sizes (e.g., Hoogland, 1995).
2. Time to first female reproduction. This was scored as 1, first reproduced as yearlings (including all species for whom it was usual); 2, first reproduced as 2 year olds; 3, first reproduced as ≥ 3 year olds.
3. Gestation time. This was the number of days from fertilization to birth.
4. Average litter size. If there was a choice, we summarized litter size at emergence from the natal burrow rather than at birth. Some *Spermophilus* data include embryo counts and may overestimate emergence litter size. Because birth mass

was generally not available, we could not calculate litter mass—a potentially better estimate of reproductive investment (e.g., Gittleman, 1989; Moehlman and Hofer, 1997).

5. Lactation time. This was the number of days from birth to weaning. Most species are weaned at emergence from their natal burrows, and many estimates were based on emergence date.

6. Percent male/female survival to age 1. We averaged male and female survival to age one. We attempted to not conflate dispersal and mortality when sufficient data were provided. Our average survival value may overestimate mortality for species that disperse in their first year of life.

7. Minimum female body mass. Early-season mean body mass was used when given. If not given, we calculated minimum mass from the first or second month's post-emergence body mass. If a range of values was given, we chose the lowest value in that range.

Regression analyses

We regressed our measure of social complexity, SC_d , against life-history variables. To control for possible phylogenetic non-independence on the life-history variables and on sociality, we examined the relationship using "standardized independent contrasts" calculated for each variable and assuming several phylogenetic hypotheses (see below). We used Purvis and Rambaut's (1995) statistical package, CAIC, to calculate independent contrasts for social complexity and each of the life-history variables. As required by the method, regressions of these standardized contrasts were through the origin. Some of these life-history variables may be influenced by body mass (e.g., Armitage, 1981; Bekoff et al., 1981; Gittleman 1989; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997; see below). To remove variation in those life-history variables that was a function of body mass, we regressed contrasts of minimum female body mass against contrasts of each variable previously reported to be influenced by mass, and used the residuals for subsequent analyses (Losos, 1990; Martins and Garland, 1991).

No published phylogenetic hypothesis includes all species of interest. We eagerly anticipate the publication of inclusive and well-supported phylogenies and report the results from five different partial working phylogenetic hypotheses. First, we generally inferred phylogeny from taxonomy (Nowak and Paradiso, 1983), but added additional information where known (Hoffmann and Nadler, 1968; Howell, 1915, for marmots; Hafner, 1984, for sciurid subgenera), and refer to this tree as "tree 1" (Figure 2). Second, because Black (1972) assumed that the genus *Marmota* evolved in the New World from a "woodchuck-like" ancestor, we switched the location of *M. marmota* and *M. monax* to create "tree 2" (Figure 2). Thomas and Martin (1993) questioned the ancestral location of the genus *Marmota*. They suggested the genus *Marmota* evolved recently from *Spermophilus* ancestors. We calculated independent contrasts from "tree 3" (Figure 2), where *Cynomys*, *Marmota*, and the remaining *Spermophilus* subgroups branch simultaneously, and "tree 4" (Figure 2), which reflected a recent origin of marmots. We generated "tree 5" (Figure 2) to recognize evidence suggesting *Cynomys* is the crown group of the subgenus *Spermophilus* in the currently recognized genus *Spermophilus* (Dobson, 1985, and references therein; Goodwin, 1990). Finally, we calculated independent contrasts with two other possible tree topologies; one suggested by R. S. Hoffmann (personal communication) and the other derived from that where *Marmota* and *Cynomys* were resolved differently. Although we do not illustrate or report results based on those trees here, the independent contrasts

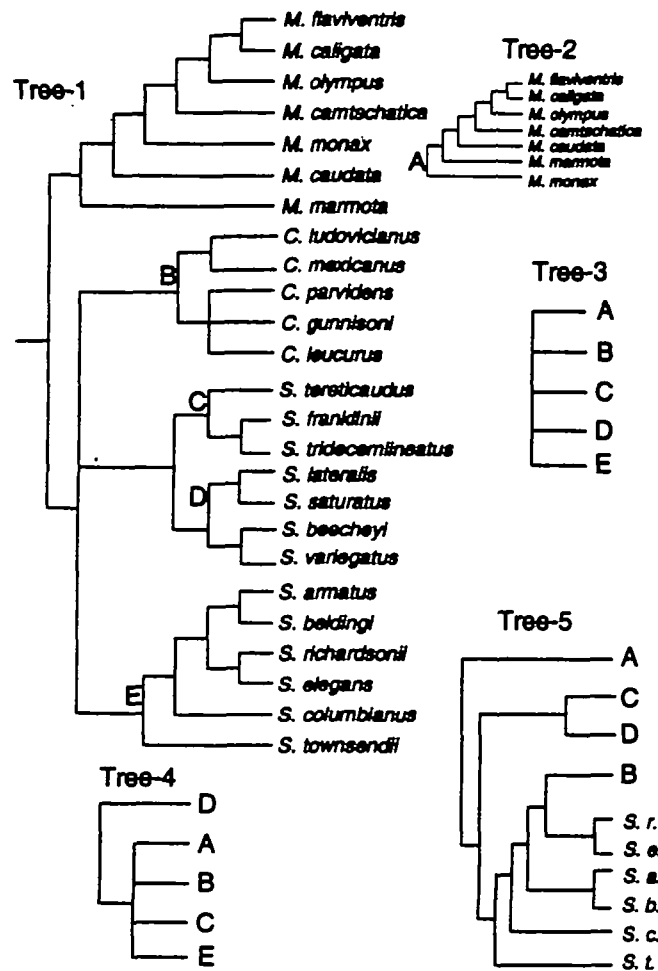


Figure 2
Phylogenetic hypotheses used to calculate contrasts. These are partial working phylogenies of sciurid rodents: recognized genera and species not included in these analyses are not illustrated. Tree 1, a taxonomically derived tree with phylogenetic information added where known. Tree 2, *Marmota monax* was shifted to reflect its possible ancestral location in *Marmota*. Letters marked at higher nodes on tree 1 and tree 2 are used to illustrate structure of the following two trees. Tree 3 illustrates an unresolved origin of *Marmota*. Tree 4 illustrates a recent origin of *Marmota* and other sciurids from a subgroup of species currently classified as *Spermophilus*. Tree 5 illustrates *Cynomys* as the crown group of the subgenus *Spermophilus*.

calculated from them led to the same conclusions as those based on trees 1–5.

To calculate standardized independent contrasts, we set all branch lengths equal and selected the “crunch” option in CAIC. Setting branch lengths equal assumes an underlying evolutionary model of punctuational change (e.g., Harvey and Pagel, 1991). In the absence of information about branch lengths, assuming punctuational change is much more straightforward than estimating an infinite number of possible branch length scenarios. Given no independent measures of branch lengths for our partial phylogenies, we did not calculate contrasts assuming Brownian motion trait evolution.

Each comparative method has strengths and weaknesses (Martins and Hansen, 1996). In addition to calculating independent contrasts, we also analyzed the data with phylogenetic autocorrelation (Cheverud et al., 1985; Gittleman and Kot, 1990; Gittleman and Luh, 1992). Phylogenetic autocorrelation permitted us to estimate and statistically remove the maximum

amount of variation in each variable (social complexity and each of the life-history variables) that could be explained by phylogenetic similarity. This is admittedly a rough metric that perhaps better quantifies the degree of evolutionary change in a clade; strictly it should not be interpreted (Losos and Miles, 1994) as the amount of adaptive versus nonadaptive trait variation (Cheverud et al., 1985). Phylogenetic autocorrelation assumes explicitly statistical models of trait change that vary according to an autoregressive model (Martins, 1995; Purvis et al., 1994) and, under a Brownian-motion model of evolution, may produce erratic results with sample sizes < 40 (Martins, 1996). We used a single phylogenetic hypothesis, the taxonomy reported in Nowak and Paradiso (1983), to estimate the “phylogenetic distance matrix.” The phylogenetic distance matrix is a “weighting matrix” that defines the relative weight that each individual species’ trait value will contribute when searching for autocorrelation. The classical taxonomic classification recognizes subgenera in both *Cynomys* and *Spermophilus* and recognizes two subtribes: one containing *Marmota* and the other containing both *Cynomys* and *Spermophilus*. We used the program “P.A.” (Luh et al., 1995) to fit phylogenetic autocorrelations.

RESULTS

Does social complexity influence the percentage of adult females who breed?

We had no a priori reason to expect that a species’ body mass should influence the proportion of females who breed. Thus, we regressed social complexity against the percentage of adult females who breed to study costs and benefits of social complexity.

No matter how we examined the relationship, more socially complex species had a smaller percentage of adult female breeders (Table 1, Figure 3). Different methods lead to different specific estimates of the amount of variation explained by social complexity (Table 1). Explained variation ranged from 24% (based on contrasts calculated using tree 4), to 58% (calculated using raw data). All methods to adjust for phylogenetic similarity reduced the amount of explained variation.

“Correlograms” (plots of Moran’s I, the autocorrelation statistic, versus taxonomic level) suggested significant autocorrelation at certain taxonomic levels that disappeared after we calculated “phylogeny-free” residuals. Phylogenetic autocorrelation results suggest a maximum of 33% of the variation in the percentage of adult females who breed may be attributed to phylogenetic similarity.

Does social complexity influence the time to first reproduction?

Body size may explain variation in the time to reproduction (Gittleman, 1989; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and time to female reproduction after removing variation in time to reproduction explained by minimum female body mass.

There is a significant, positive relationship between social complexity and the time to first reproduction (Table 1, Figure 4). More social species first breed at older ages. Interestingly, after removing variation in the time to reproduction accounted for by body mass, analyses based on independent contrasts and phylogeny-free residuals both explained more variation than the analyses on nonindependent raw data. As much as 75% of the variation in time to first reproduction was explained by social complexity (in the contrasts analysis using tree 3).

Table 1
Variation explained by social complexity

	Trend	Raw data	Raw mass-free data	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Autocorrelation
Percent females breed	-	0.58	—	0.41	0.25	0.26	0.24	0.36	0.48
Time to first reproduction	+	0.50	0.20	0.61	0.53	0.75	0.51	0.53	0.67
Gestation time (days)		0.22	0	0.04	0.19	0.10	0.03	0.15	0
Average litter size	-	0.37	0.22	0.14*	0.19	0.28	0.22	0.21	0.21
Lactation time (days)		0	0	0	0	0	0	0	0
Survival to age 1	+	0.34	—	0.32	0.34	0.36	0.30	0.24	0.33

Variation explained by social complexity (adjusted R^2 , bold if $p < .05$) for six life-history traits analyzed different ways. Trend is the direction of significant trends (+ or -). Raw data is the variation in the dependent variable explained by social complexity from regressions of the raw data. Raw mass-free data is the variation explained by sociality after variation explained by body mass has been removed from the dependent variable. Tree 1, 2, 3, and 4 are results calculated by regressing independent contrasts of social complexity against the independent contrasts of each dependent variable. The values differ in the phylogenetic hypotheses used to calculate contrasts. Autocorrelation is the result of regressing phylogeny-free residuals of sociality against each dependent variable. If there is a value in the raw mass-free data column, then analyses are conducted on mass-free residuals (see text for details).

* $p = .0519$.

Correlograms suggested significant autocorrelation at all taxonomic levels that disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest a maximum of 60% of the variation in the time to first female reproduction may be attributed to phylogenetic similarity.

Does social complexity influence gestation time?

Body size may explain variation in gestation time (Armitage, 1981; Bekoff et al., 1981; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and gestation time after removing variation in gestation time explained by minimum female body mass.

Although there is a significant positive relationship between social complexity and gestation time in the raw data set, after controlling for body mass, social complexity explained no significant variation in gestation time (Table 1, Figure 5). Phy-

logenetically based analyses produced mostly consistent, negative results: 19% of the variation was explained in contrast analysis using tree 2, and 15% using tree 5 (Table 1). All other phylogenetically based analyses found no significant relationship between social complexity and gestation time.

Correlograms suggested significant autocorrelation at sub-tribe and tribe taxonomic levels, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest that a maximum of 47% of the variation in the gestation time may be attributed to phylogenetic similarity.

Does social complexity influence litter size?

Body size may explain variation in average litter size (Armitage, 1981; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and average litter size after removing variation in litter size explained by minimum female body mass.

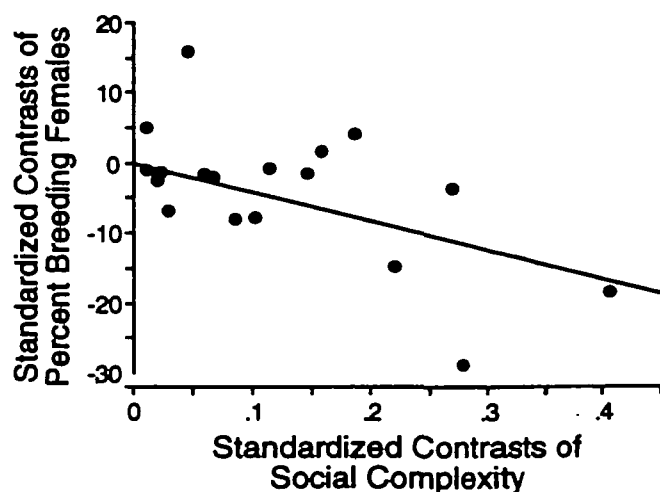


Figure 3
The relationship between standardized contrasts of social complexity and standardized contrasts of the percentage of adult females who breed. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

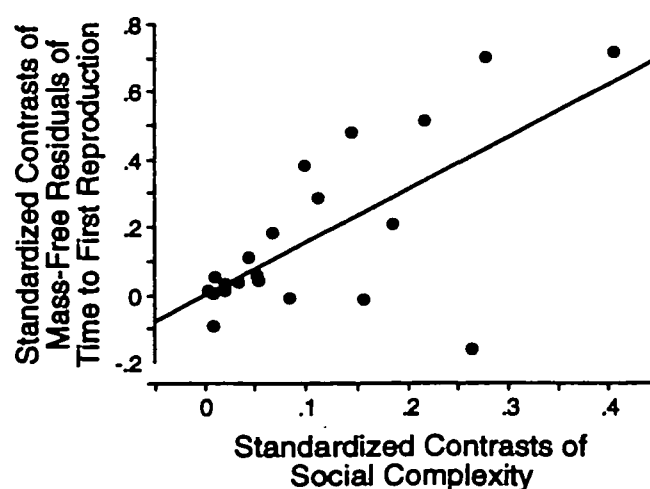


Figure 4
The relationship between standardized contrasts of social complexity and standardized contrasts of the body mass-free residuals of time to first female reproduction. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

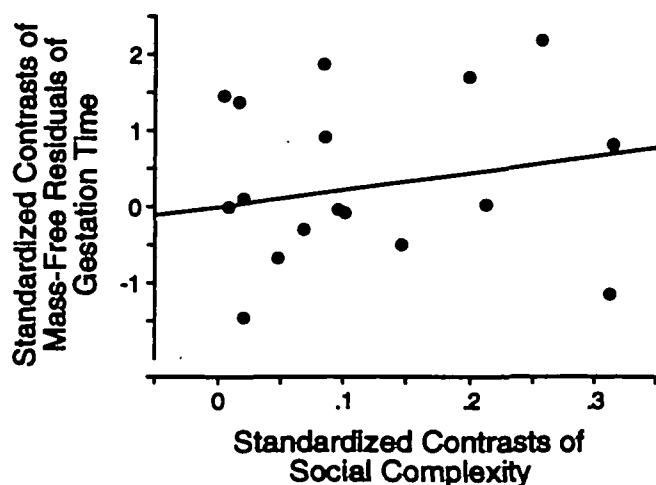


Figure 5
The relationship between standardized contrasts of social complexity and standardized contrasts of the body mass-free residuals of gestation time. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

There is a significant, negative relationship between social complexity and average litter size (Table 1, Figure 6). More social species have smaller litters. After controlling for variation accounted for by body mass, 14–28% of the variation in litter size was explained by social complexity in contrast-based analyses, and 21% was explained by social complexity after removing the effects of phylogeny in the autocorrelation analysis.

Correlograms suggested significant autocorrelation at all but the subgenus taxonomic level, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest that a maximum of 17% of the variation in average litter size may be attributed to phylogenetic similarity.

Does social complexity influence lactation time?

Body size may explain considerable variation in lactation time (Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and lactation time after removing variation in lactation time explained by minimum female body mass.

There is no relationship between social complexity and lactation time (Table 1, Figure 7). All analyses produced consistent results: no variation in lactation time was explained by social complexity.

Correlograms suggested no significant autocorrelation at any of the taxonomic levels we examined. Thus, we could not estimate the amount of variation in lactation time explained by phylogenetic similarity.

Does social complexity influence juvenile survival to age 1?

We had no a priori reason to expect that a species' body mass should influence survival to age 1. Thus, we regressed social complexity against overall survival to age 1 to study costs and benefits of social complexity.

No matter how we examined the relationship, more socially complex species had a higher survival rate to age one (Table 1, Figure 8). Different methods lead to different estimates of the amount of variation explained by social complexity (Table

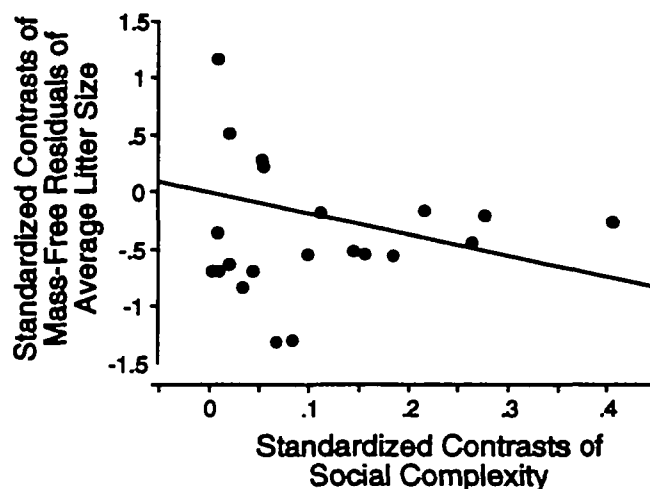


Figure 6
The relationship between standardized contrasts of social complexity and standardized contrasts of the body-mass free residuals of the average litter size. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

1). About 30% of the variation in survival to age one (range 24–36%) was explained by social complexity.

Correlograms suggested significant autocorrelation at the tribe level, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation suggested a maximum of 4% of the variation in survival to age 1 was explained by phylogenetic similarity.

DISCUSSION

To our knowledge, this is the first study to specifically examine life-history consequences of social complexity. Moreover, and

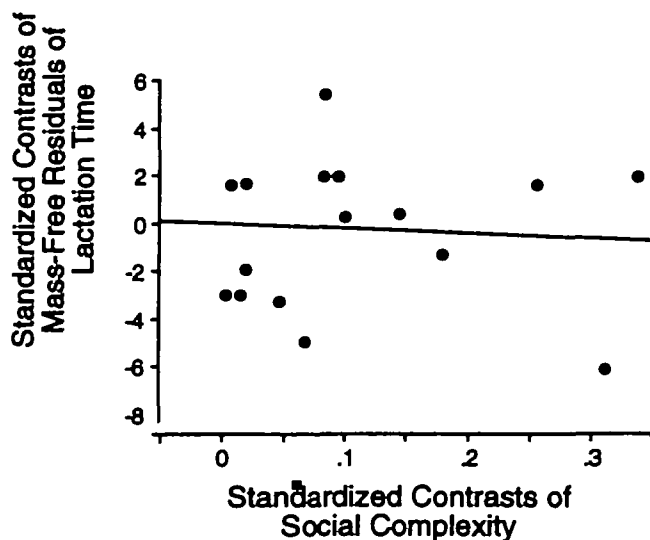


Figure 7
The relationship between standardized contrasts of social complexity and standardized contrasts of the body-mass free residuals of lactation time. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

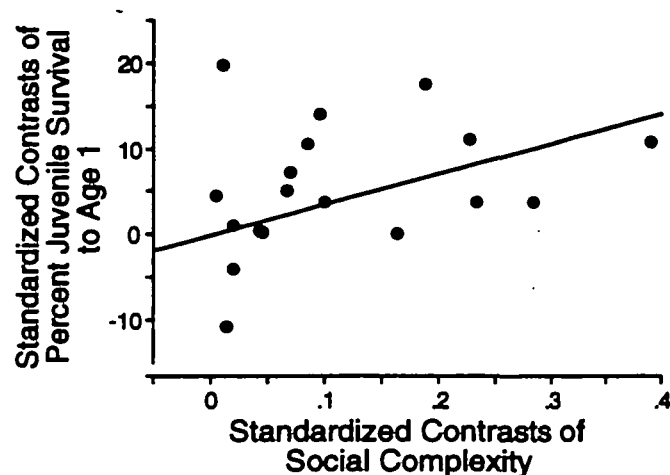


Figure 8

The relationship between standardized contrasts of social complexity and standardized contrasts of the percent juvenile survival to age 1. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

unlike other current studies of complexity, we focused on the consequences of complexity rather than on the evolution of complexity itself (e.g., Bonner, 1988; McShea, 1991, 1996; Szathmáry and Maynard Smith, 1995). As sciurid social complexity increased, a smaller proportion of adult females bred (Figure 3), age of first reproduction increased (Figure 4), litter size decreased (Figure 6), and first-year offspring survival increased (Figure 8). Social complexity influenced neither gestation time (Figure 5) nor lactation time (Figure 7). Thus, social complexity has costs in terms of a reduction in the annual per capita number offspring produced, but benefits in terms of enhanced offspring survival.

It is not surprising that gestation and lactation time were unaffected by social complexity. The times of gestation and lactation are correlated with body size in mammals, but the correlation with lactation is weak (Reiss, 1989). Gestation, but not lactation, is correlated with body size in ground-dwelling sciurids (Armitage, 1981). Both of these life-history variables are more likely dependent on the physiological processes of converting maternal energy into neonate energy. For example, relative birth weight is proportional to adult metabolic rate and the relative cost of producing an offspring is similar for large and small mammals (Rahn, 1982). Because milk production and energy content of milk can vary widely, the time of lactation can vary with environmental conditions (Peaker et al., 1984). Among ground-dwelling sciurids, the period of lactation was positively correlated with the length of the active season. For example, *M. monax*, with an active season of about 8.5 months, has a lactation period of 46 days, whereas *M. flaviventris*, with an active season of about 4.5 months, has a lactation period of 24 days (Armitage, 1981; this study).

The inclusion of phylogenetic information to the comparative study generated remarkably consistent results. Given some uncertainty about historical relationships, we examined several phylogenetic hypotheses and two different comparative methods; all led to consistent and interpretable results which in some cases differed from analyses on raw data (see Purvis et al., 1994; but also see Ricklefs and Stark, 1996). While we acknowledge more data and better phylogenetic resolution will permit better estimates of the exact relationship between social complexity and these life-history variables, we

suspect, given the variety of hypotheses examined, they will not change the major conclusions.

Armitage (1981) first suggested that sociality is a life-history tactic in sciurid rodents. Both Armitage (1981) and Barash (1989) noted that increased sociality reduces juvenile mortality by retention of juveniles in the social groups. Our comparative evidence suggests that this pattern is widespread among ground-dwelling sciurids: more socially complex species have a greater percentage of juveniles survive to age 1. Arnold's (1993b) studies of thermoregulatory helping behavior during hibernation in marmosets provides direct evidence that, by delaying dispersal, offspring can increase the survival of their younger siblings. We predict that more social species will have more kin-selected (Hamilton, 1964) mechanisms to increase offspring survival. We acknowledge that kin selection may also work on a larger spatial scale, and behaviors such as alarm calls may benefit relatives not living in the same social group (e.g., Sherman, 1977; but see Blumstein et al., 1997).

Sociality has its costs in terms of the ability to produce offspring. As social complexity increased in sciurid rodents, fewer females bred. After controlling for variation accounted for by body size, we found that more socially complex species took longer to first reproduce and had smaller litters. These patterns suggest that some form of reproductive suppression should be common in more socially complex sciurid rodents, and perhaps more generally, in more social species. Certainly, some of the most remarkable forms of reproductive suppression occur in highly social species with numerous roles within a society (e.g., *Heterocephalus glaber*; Faulkes et al., 1991; social insects: Brockmann, 1984).

Additional demographic evidence exists for reproductive suppression. Among several marmot species, the percentage of females breeding increases with age. When older females are removed from the population, or when the population density is low, younger females breed (Armitage, 1996). In the biennial breeding *M. caligata*, a female skips an additional year when her co-resident breeds (Wasser and Barash, 1983). In *M. flaviventris*, weaning success is lower for females living in proximity to other adult females than in those living with no other adult females (Armitage, 1986).

The reproductive costs of sociality raise the question of why reproductively suppressed females remain in social groups. Several possibilities come to mind. First, survivorship of dispersers is likely to be less than those who become reproductive on their natal home range because dispersers are more susceptible to predation than are residents (Hoogland, 1995; Van Vuren and Armitage, 1994). Second, dispersers must either colonize new habitat or invade an established group. Immigrants encounter resistance and may receive wounds inflicted by residents (Garrett and Franklin, 1988). Consequently, immigration rates may be low (Sherman and Morton, 1984), and immigration into "higher-quality" habitat patches may not occur annually (Armitage, 1984, 1991). For most *M. flaviventris* social groups, recruitment (retention of individuals in their natal social group) greatly exceeds immigration; immigration is likely to occur only when resident mortality is high and unoccupied areas are available for settlement (Armitage, 1988). In those species with low social complexity and high rates of population turnover (e.g., *S. beldingi*; Sherman and Morton, 1984; *S. richardsonii*; Michener and Michener, 1977), individuals that survive hibernation have a high probability of finding vacant space and breeding. However, some species with high social complexity have a low rate of population turnover, thus *M. flaviventris* (Armitage, 1988, 1991), *C. ludovicianus* (Hoogland, 1995), and *M. olympus* (Barash, 1973) habitats may approach saturation (Armitage, 1996). For socially complex species, an individual's probability of future reproduction may increase by remaining in its natal habitat rather

than dispersing in an attempt to reproduce at a younger age. However, individuals should disperse when the costs of remaining in their natal group are greater than the costs of dispersing. If nonbreeding residents can gain indirect fitness, delayed dispersal may be favored (e.g., Arnold, 1995). Dispersal should be delayed to an age when the probability of successful colonization is greater than that of dispersing at a younger age (Armitage, 1992).

Several factors should enter into the decision-making process of whether to disperse or to remain philopatric. Decisions may differ between the sexes depending on which sex normally disperses. In most species of ground-dwelling squirrels, natal dispersal is male biased and males typically disperse in the season before attaining reproductive maturity (Holekamp, 1984). Female dispersal is more variable, and, in squirrels, females tend to be philopatric or to disperse shorter distances than males (Armitage, 1981; Holekamp, 1984; Michener, 1983). Thus, conspecific density may serve as an important cue to the likelihood of successful settlement and eventual reproduction. However, the timing of dispersal should depend on an individual's expected life span; individuals of species with longer life spans and older ages at reproductive maturity are better able to delay dispersal. The probability of finding and being capable of occupying a vacant habitat should, on average, increase as an animal becomes older. But for any particular individual, that probability will be affected by the demographic events occurring in its social group in the years before its birth, which will affect the likelihood of becoming resident, and by demographic events in other social groups, which will effect the likelihood of immigration. Furthermore, each individual's residual reproductive value, which initially increases, will begin to decline at some point. When residual reproductive value declines, individuals should attempt to maximize their remaining reproductive value. Whether individuals remain in their natal group will depend on the level of inbreeding tolerance, the presence of dominant conspecifics, and the distance to neighboring groups. If groups are widely dispersed such that the probability of find-

ing a group with a vacancy is low, the potential fitness cost of inbreeding and/or further loss of residual reproductive value may be less than the costs of dispersing. Where groups are contiguous or closely spaced individuals may easily and inexpensively determine vacancies in neighboring groups. Individuals should disperse if the expected fitness of moving is greater than the expected fitness from remaining at home for 1 or more additional years before breeding. Finally, when residual reproductive value is declining, animals that disperse should make a greater effort to invade and displace a resident; conversely, an animal that remains in its natal social group should attempt to become reproductive.

We do not envision social complexity as a direct target of selection. Social complexity, per se, does not evolve; we envision no "complexity genes." Rather, social complexity emerges following the evolution of social roles and social behaviors (*sensu* Hinde, 1975). Social complexity is a descriptive concept that allows us to study broad relationships and compare species-specific adaptations with a common currency. Detailed study of each species is required to document mechanisms of increased offspring survival and mechanisms of reproductive suppression. Here and elsewhere (Blumstein and Armitage, 1997) we compared the social complexity among species. Our method of quantifying social complexity also can be used to quantify intraspecific variation in social complexity, and thus may be useful in intraspecific socioecological studies (Lott, 1991).

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APPENDIX

Social complexity and life history variables summarized from the sciurid literature

Species	Social complexity	Minimum female mass (g)	% Females breeding	Time to first female reproduction (years)	Gestation time (days)	Lactation time (days)	Average litter size	References*
<i>M. flaviventris</i>	1.06	2560	48	2	29	24	4.3	1-12
<i>M. caligata</i>	1.35	3300	45	3	30	28	3.0	13-18
<i>M. olympus</i>	1.46	1400	45	3	nd	nd	4.0	19
<i>M. camtschatica</i>	1.10	nd	nd	3	nd	nd	4.3	20-22
<i>M. monax</i>	0.27	3314	95	1	34	46	4.0	23-31
<i>M. caudata</i>	1.22	1400	14	3	30	nd	4.2	32-33
<i>M. marmota</i>	1.41	2811	48	3	37	45	2.4	23, 34-38
<i>C. ludovicianus</i>	1.12	525	75	1	34	41	3.1	39-41
<i>C. mexicanus</i>	1.05	756	nd	1	nd	40	4.4	42-43
<i>C. parvidens</i>	1.23	703	80	1	nd	nd	3.9	44-45
<i>C. gunnisoni</i>	1.03	600	66	1	29	39	4.6	46-51, 127
<i>C. leucurus</i>	0.84	575	88	1	30	35	5.6	52-56, 128
<i>S. tereticaudus</i>	0.48	100	90	1	28	28	6.5	57-63
<i>S. franklinii</i>	0.41	333	63	1	28	28	7.5	64-66
<i>S. tridecemlineatus</i>	0.50	105	95	1	28	32	7.3	67-74
<i>S. lateralis</i>	0.38	120	nd	1	31	35	5.0	75-77
<i>S. saturatus</i>	0.27	184	100	1	28	43	4.1	23, 78-80
<i>S. beecheyi</i>	0.26	486	90	1	28	38	7.5	81-86
<i>S. variegatus</i>	0.43	546	74	1	30	49	4.8	87-90
<i>S. armatus</i>	0.44	180	90	1	24	21	5.4	91-94
<i>S. beldingi</i>	0.40	211	95	1	27	25	4.2	95-99

continued

APPENDIX

Continued

Species	Social complexity	Minimum female mass (g)	% Females breeding	Time to first female reproduction (years)	Gestation time (days)	Lactation time (days)	Average litter size	References*
<i>S. richardsonii</i>	0.39	269	95	1	22	29	6.8	23, 100–107
<i>S. elegans</i>	0.43	189	nd	1	22	32	5.9	108–111
<i>S. columbianus</i>	0.65	376	75	2	24	28	3.7	112–123
<i>S. townsendii</i>	0.41	93	86	1	24	38	8.6	124–126

nd, no data. All variables defined in text.

- * 1, Armitage, 1965; 2, Armitage, 1974; 3, Armitage, 1975; 4, Armitage, 1984; 5, Armitage, 1991; 6, Armitage and Downhower, 1974; 7, Armitage and Johns, 1982; 8, Armitage et al., 1979; 9, Brody AK, and Melcher J, personal communication; 10, Frase and Hoffmann, 1980; 11, Schwartz et al., unpublished data; 12, Thompson, 1979; 13, Barash, 1974; 14, Barash, 1980; 15, Barash, 1981; 16, Holmes, 1979; 17, Holmes, 1984b; 18, Holmes, 1984a; 19, Barash, 1973; 20, Kapitonov, 1963 cited in Rausch and Rausch, 1971; 21, Mosolov and Tokarsky, 1994; 22, Ognev, 1947; 23, Arnold, 1993a; 24, Meier, 1985; 25, Meier, 1992; 26, Davis et al., 1964; 27, de Vos and Gillespie, 1960; 28, Ferron and Ouellette, 1989; 29, Grizzell, 1955; 30, Snyder, 1962; 31, Snyder and Christian, 1960; 32, Blumstein DT, unpublished data; 33, Blumstein and Arnold, in press; 34, Arnold, 1990; 35, Arnold, 1993a; 36, Barash, 1976; 37, Perrin et al., 1993b; 38, Perrin et al., 1993a; 39, Hoogland, 1995; 40, King, 1955; 41, Knowles, 1987; 42, Ceballos-G. and Wilson, 1985; 43, Trevino-Villarreal, 1990; 44, Pizzimenti and Collier, 1975; 45, Wright-Smith, 1978; 46, Fitzgerald and Lechleitner, 1974; 47, Longhurst, 1944; 48, Pizzimenti and Hoffmann, 1973; 49, Rayor, 1985; 50, Rayor, 1988; 51, Rayor and Armitage, 1991; 52, Clark, 1977; 53, Clark et al., 1971; 54, Cooke L, personal communication; 55, Stockard, 1929; 56, Tileston and Lechleitner, 1966; 57, Dunford, 1977b; 58, Dunford, 1977c; 59, Dunford, 1977a; 60, Ernest and Mares, 1978; 61, Neal, 1965a; 62, Neal, 1965b; 63, Reynolds and Turkowski, 1972; 64, Iverson and Turner, 1972; 65, Murie, 1973; 66, Sowls, 1948; 67, Armstrong, 1972; 68, McCarley, 1966; 69, McCarley, 1970; 70, Rongstad, 1965; 71, Schwagmeyer, 1980; 72, Schwagmeyer and Brown, 1983; 73, Streubel and Fitzgerald, 1978; 74, Wistrand, 1974; 75, Bartels and Thompson, 1993; 76, Bronson, 1979; 77, Hart, 1927; 78, Kenagy and Barnes, 1988; 79, Trombulak, 1987; 80, Trombulak, 1988; 81, Dobson and Davis, 1986; 82, Dobson, 1979; 83, Dobson, 1983; 84, Evans and Holdenried, 1943; 85, Fitch, 1948; 86, Holekamp, 1989; 87, Oaks et al., 1987; 88, Ortega, 1990a; 89, Ortega, 1990b; 90, Shriner and Stacey, 1991; 91, Balph, 1984; 92, Balph and Stokes, 1963; 93, Sauer and Slade, 1987; 94, Slade and Balph, 1974; 95, Jenkins and Eshelman, 1984; 96, Morton, 1975; 97, Morton and Gallup, 1975; 98, Morton and Farmer, 1975; 99, Sherman and Morton, 1984; 100, Michener, 1979a; 101, Michener, 1979c; 102, Michener, 1979b; 103, Michener, 1980; 104, Michener and Koeppl, 1985; 105, Michener and Locklear, 1990; 106, Michener and Michener, 1977; 107, Yeaton, 1972; 108, Faggerstone, 1982 cited in Zegers, 1984; 109, Pfeifer, 1982; 110, Zegers, 1984; 111, Zegers and Williams, 1977; 112, Balfour, 1983; 113, Boag and Murie, 1981; 114, Elliot and Flinders, 1991; 115, Festa-Bianchet, 1981; 116, Festa-Bianchet and Boag, 1982; 117, Festa-Bianchet and King, 1984; 118, Festa-Bianchet and King, 1991; 119, Betts, 1976; 120, Murie and Harris, 1978; 121, Murie and Harris, 1982; 122, Young, 1990; 123, Zammuto and Millar, 1985; 124, Smith and Johnson, 1985; 125, Rickart, 1986; 126, Rickart, 1987; 127, Hoogland, in press; 128, Dobson S, and Hadlock T, personal communication.

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